

Habitat-based conservation strategies cannot compensate for climate-change-induced range loss

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Anthropogenic habitat fragmentation represents a major obstacle to species shifting their range in response to climate change¹. Conservation measures to increase the (meta-)population capacity² and permeability of landscapes³ may help but the effectiveness of such measures in a warming climate has rarely been evaluated. Here, we simulate range dynamics of 51 species from three taxonomic groups (vascular plants, butterflies and grasshoppers) in Central Europe as driven by twenty-first-century climate scenarios and analyse how three habitat-based conservation strategies (establishing corridors, improving the landscape matrix, and protected area management) modify species' projected range size changes. These simulations suggest that the conservation strategies considered are unable to save species from regional extinction. For those persisting, they reduce the magnitude of range loss in lowland but not in alpine species. Protected area management and corridor establishment are more effective than matrix improvement. However, none of the conservation strategies evaluated could fully compensate the negative impact of climate change for vascular plants, butterflies or grasshoppers in central Europe.

Plants and animals are shifting their ranges in response to recent climate change^{4,5} and the climate predicted for the twenty-first century will further increase pressure on species to shift their geographical distributions⁶. In many terrestrial environments, however, human-modified landscapes offer little space for the establishment of new populations and impede the redistribution of species^{7,8}. Indeed, empirical evidence suggests that species frequently prefer high-quality habitats as offered by protected areas when expanding their ranges⁹. As a consequence, increasing the quality, quantity and connectivity of habitats appears pivotal for mitigating negative impacts of climate change on biodiversity^{3,10}.

Three important approaches for the spatial allocation of habitat-based climate change adaptation measures are: increasing the conservation value of the existing protected area network—that is, improving habitat quality and/or management efficiency within protected areas¹¹; establishing high-quality habitat corridors to enhance connectivity among protected areas¹²; and improving the habitat quality and permeability of the 'average' landscape matrix, for example, by establishing interspersed high-quality habitat patches such as low-intensity grasslands, hedgerows, marginal field strips or (semi-)natural forest patches¹³. In Europe, each of these conservation strategies has recently been integrated into

spatial planning and land use policies such as the European Habitats Directive¹⁴, the European Union Green Infrastructure strategy¹⁵, the European Union agriculture policy, and ecosystem restoration goals¹⁶. However, whether these strategies mitigate climate-change-driven range loss of species remains little tested so far¹⁷.

Here, we used coupled niche-demographic modelling¹⁸ (see Supplementary Fig. 1) to assess regional range loss and extinction risk of 51 species from three taxonomic groups (vascular plants, butterflies, grasshoppers) under current climatic conditions and two climate change scenarios (B2—mild scenario, A1B—moderately pronounced scenario) in Central Europe (Austria, Switzerland, Liechtenstein, Northern Italy and southern Germany, Supplementary Fig. 2). We thereby compared a 'business-as-usual' setting (that is, current spatial habitat patterns remain unchanged) with three conservation strategies: improving protected area management (P), establishing corridors (C) and improving the landscape matrix (M). The 51 species represent a wide range of ecological profiles (Supplementary Tables 1–3) and have their current elevational distribution centred either in the colline to montane (henceforth termed lowland species) or the subalpine to alpine belt (alpine species; 7–10 species from each elevational group per taxon depending on model quality—see Supplementary Methods). Conservation strategies were implemented by modifying a gridded habitat distribution map (spatial grain 100 × 100 m; in the following, cells of this grid are called 'sites') of the study region¹⁹—that is, by converting a proportion of intensively used habitats (agricultural fields, nutrient-rich grasslands, conifer plantations) to extensively used semi-natural ones (for example, dry grasslands, wet grasslands, broadleaved forests). We applied three effort levels: low (that is, 1% of sites being converted), medium (3%) and high (5%). Conservation strategies differed in the spatial arrangement of habitat conversion. In P (protected areas) and C (corridors) conversion was restricted to protected areas or to protected areas and connecting corridors, respectively (Supplementary Fig. 2). In M (matrix), converted habitats were randomly distributed across the landscape. We evaluated the effectiveness of these strategies as compared to the business-as-usual strategy by simulating changes in range size of the study species until the year 2090. To account for uncertainties in the estimation of the species' demographic and dispersal rates, all simulations were run using two sets of parameters, one at the upper and one at the lower end of documented parameter ranges (Supplementary Tables 2 and 3).

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Table 1 | Predicted climate-induced range loss of species.

		Plants	Butterflies	Grasshoppers
Lowland species	Pronounced warming (A1B)	64%/73%	73%/77%	71%/49%
	Mild warming (B2)	66%/74%	73%/80%	73%/80%
Alpine species	Pronounced warming (A1B)	41%/47%	46%/51%	49%/51%
	Mild warming (B2)	41%/51%	12%/28%	24%/33%

Values represent the range size predicted for 2090 in percentage of current range size. The first and second values represent predictions achieved with dispersal and demographic parameters at the upper and lower end of the documented range, respectively.

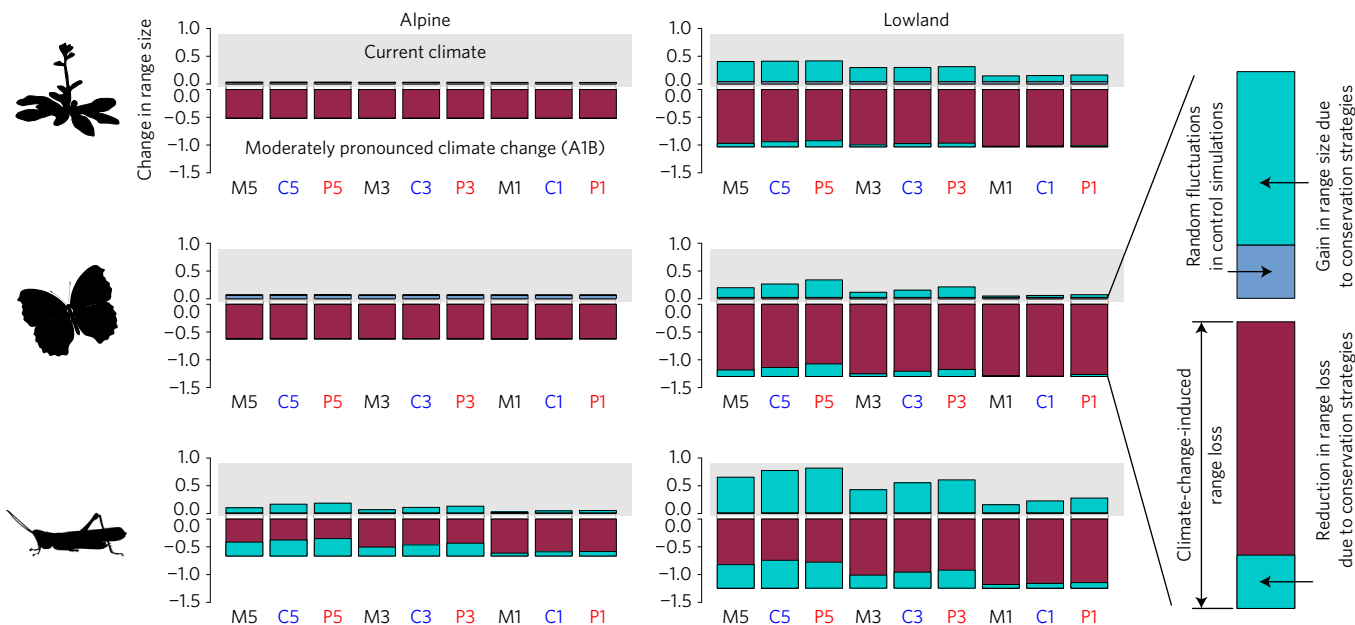


Figure 1 | Mean effects of current climate/moderately pronounced climate change (turquoise bars) and of conservation strategies (red bars) on species range size until the end of the twenty-first century. Effects of climate change were calculated as $\log(\text{range size at 2090}/\text{range size at 2010})$ and effects of conservation strategies as $\log(\text{range size in 2090 applying a conservation strategy}/\text{range size in 2090 under the business-as-usual strategy})$, respectively. Thus negative values denote range loss, and positive values denote range gain. Results of simulations assuming current climatic conditions to be stable during the twenty-first century are indicated by a grey background, while bars in front of a white background are results of simulations which assume climate change according to the A1B scenario. Results are similar for mild (B2) climate change (Supplementary Fig. 4). Conservation strategies were applied by converting intensively used habitats into habitats of high conservation value within protected areas (P; red label text), within corridors connecting protected areas (C; blue) and within the landscape matrix (M; black). For each conservation strategy, three levels of effort were analysed: low (that is, 1% of sites were converted; represented by P1, C1, M1), medium (3%; represented by P3, C3, M3) and high (5%; represented by P5, C5, M5). Results were averaged over five simulation runs. Species predicted to be committed to extinction until 2090 were excluded from the analysis. Demographic rates were assumed to be at the upper end of the documented range. Number of species: 9 alpine/8 lowland, 8/7 and 5/4 for plants, butterflies and grasshoppers, respectively (see Supplementary Table 1). Results of simulations using the lower parameter set are given in Supplementary Fig. 5.

Under unchanged climatic conditions and without any conservation measures, our simulations resulted in approximately constant range sizes of all model species until the end of the century (Supplementary Fig. 3). With climate warming, however, about one in five species was predicted to go regionally extinct under both the mild (1 alpine/0 lowland, 1/1 and 3/3 species for plants, butterflies and grasshoppers, respectively) and moderately pronounced scenario (1/1, 1/0 and 3/4 species for plants, butterflies and grasshoppers, respectively). Modelled conservation strategies and efforts had no effect on the fate of these species: none of them was rescued, even under the highest effort levels.

For those species not going extinct (9 alpine/9 lowland plants, 8/6 butterflies and 5/5 grasshoppers under B2 and 9/8, 8/7 and 5/4 under A1B), climate change triggered a reduction in range size which was, on average, similarly pronounced under the A1B (mean: 58% and 61% under the high and low demographic and dispersal parameter sets, respectively) and the B2 scenario (52%/62%), but

much stronger for lowland than for alpine species (Table 1). Conservation strategies were more effective in reducing range loss than in avoiding extinction with, again, pronounced differences between lowland and alpine species as well as between taxonomic groups (Fig. 1 and Table 2 and Supplementary Figs 4 and 5). Efficiency was highest for grasshoppers, less marked in the case of lowland butterflies and lowland plants, and marginal in the case of alpine butterflies and alpine plants. In addition, positive effects of conservation strategies were substantially weaker for forest species than for grassland species (Supplementary Fig. 6). Among grassland species, those of dry and extensive grasslands responded more strongly to conservation strategies than those of wet grasslands.

Under low demographic and dispersal parameters, increasing conservation efforts had only marginal to weak consequences for simulated range loss under climate change (Supplementary Fig. 5). Under high values of demographic and dispersal parameters, by contrast, increasing the effort also increased the impact

Table 2 | Mean effect of management measures on predicted future range sizes of species under moderately pronounced climate warming (A1B).

	Plants	Butterflies	Grasshoppers
Lowland species	5.5%/1.5%	10.0%/0.0%	33.6%/2.1%
Alpine species	0.0%/0.0%	0.0%/0.0%	20.6%/3.6%

Values represent percentage increase of predicted range size in 2090 as compared to a business-as-usual strategy (that is, no management) and are averages over three conservation strategies (protected area, corridor, matrix) applied at three effort levels (low/medium/high). The first and second values represent predictions achieved with dispersal and demographic parameters at the upper and lower end of the documented range, respectively.

of conservation measures: for about every fifth lowland grasshopper species, high conservation efforts resulted in late twenty-first-century ranges at least twice as large as under the business-as-usual strategy (Fig. 2). Anyway, for none of the taxonomic groups even the combination of highest level conservation efforts and high parameter choices resulted in full compensation of climate-change-induced average range loss (Fig. 1). Species benefited most from conservation measures under current climatic conditions. Measured effectiveness differed moderately, but statistically significantly, among the three conservation strategies ($P > C > M$; Table 3). Differences were more significant with low than with high conservation effort (Table 3).

Taken together, our simulations suggest that regional ranges of all modelled species will decline under a warming climate, and that the efficiency of the tested conservation strategies for halting this decline is limited. However, effects vary considerably among species, with a marked difference among those of low and high elevations. The likely reason is that semi-natural habitats are restricted to remnant patches in Central European lowlands while they still represent the matrix at (sub-) alpine elevations. As a consequence, habitat restoration has ample scope in lowlands but limited potential in high mountain landscapes. In addition, most alpine species are unable to survive in forests. Improving connectivity for their above-treeline habitats would hence require the replacement of subalpine or montane forests, including natural ones, by non-forest habitat types—that is, an increasing intensity of human land use rather than restoring the (semi-)natural forest vegetation of these elevations²⁰.

Even for lowland species, the success of conservation measures is mixed, but improving habitats in protected areas or connecting protected areas via corridors was generally more efficient than randomly distributing high-quality habitats across the landscape. This difference indicates that spatial coherence of suitable habitat is important for species' survival and range adaptation (Supplementary Fig. 2). Put another way, random placement of habitat patches in an intensively used matrix leaves gaps among potential stepping stones which apparently are often too large for the 'average' dispersal capacity of plant or insect species. The

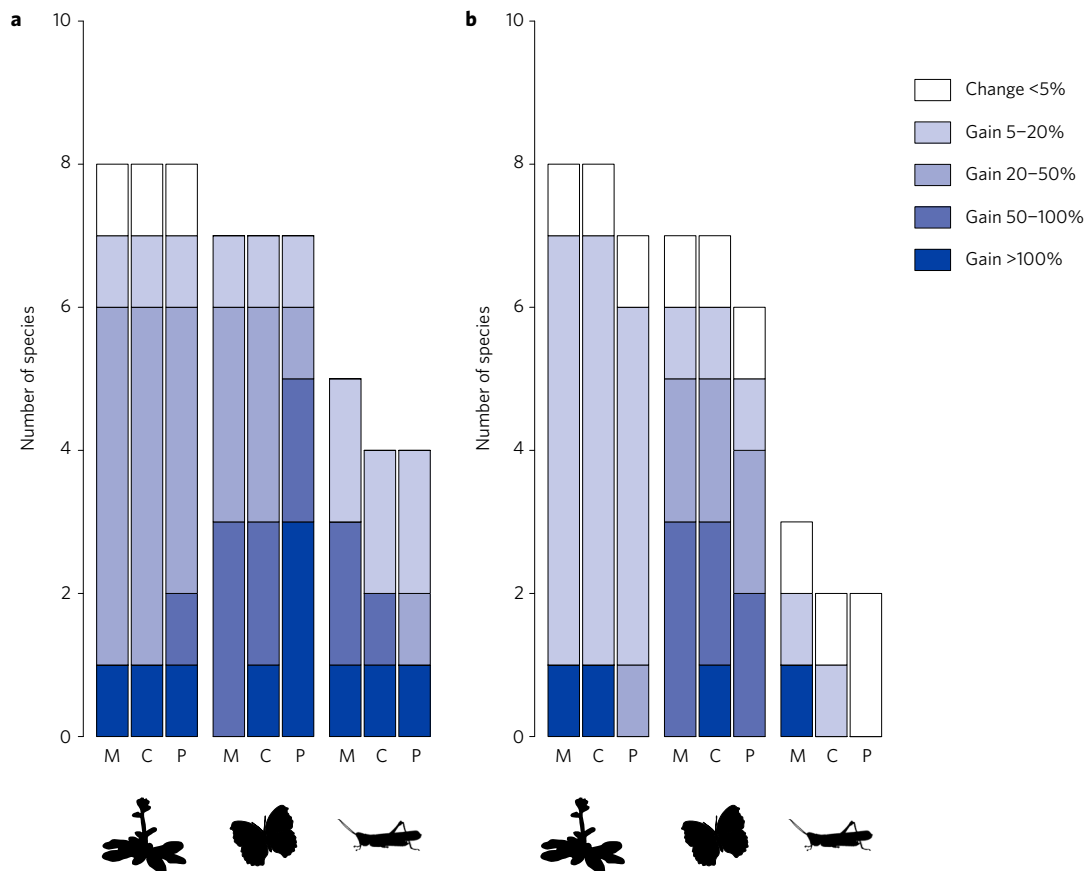


Figure 2 | The effect of implementing high effort conservation strategies (that is, conversion of 5% of intensively used habitats into extensively used ones) on projected range sizes of lowland species. a, b. Changes in range size are calculated for the year 2090 by comparing the area simulated to be occupied under a high conservation effort strategy with the area simulated to be occupied under a business-as-usual strategy (that is, no habitat conversion), under either the current climate (a) or moderately pronounced climate change (A1B; b). The proportion of species is given for protected areas (P), corridors (C) and landscape matrix (M) conservation strategies. Results were averaged over five simulation runs. Results assuming mild (B2) climate change are similar to those of pronounced climate change and, hence, not shown.

Table 3 | Differences in effects of three conservation strategies (protected area, corridor, and matrix) on predicted future lowland species' range size for three levels of conservation effort (low/medium/high) under current climate and two climate change scenarios.

	Corridor–Matrix Low/medium/high	Protected area–Matrix Low/medium/high	Protected area–Corridor Low/medium/high
Current climate	0.009/0.081/0.041	0.008/0.001/0.014	0.018/0.035/0.221
Mild warming (B2)	0.002/0.002/0.134	0.009/0.005/0.014	0.506/0.996/0.181
Pronounced warming (A1B)	0.164/0.097/0.340	0.018/0.005/0.028	0.546/0.077/0.630

Effects of conservation strategies are calculated as log (range size in 2090 applying a conservation strategy/range size in 2090 under the business-as-usual strategy). Values are means across species. Positive values indicate that the effect of the strategy given first in the column header is higher. Significant differences between strategies are indicated in bold (paired Wilcoxon Rank Sum Tests applying Bonferroni corrections for multiple comparisons). Values refer to simulations with dispersal and demographic parameters at the upper end of the documented range. Values achieved with parameters at the lower end are given in Supplementary Table 6.

spatially condensed habitat conversion under P and C, by contrast, targets those parts of the study region which offer most high-quality patches already today (that is, protected areas) and hence removes dispersal barriers within and between these hotspots of current species distribution.

Lower effectiveness of conservation measures under climate warming is probably due to limited dispersal abilities. An increased temperature forces species to expand their ranges at the front edge of their distribution to track the shifting climate and compensate losses at the rear edge⁷. The required velocity may easily be beyond species dispersal capacity even in continuous habitats⁸, a situation far from being reached in our study area even under highest conservation efforts (Supplementary Fig. 2). As a consequence, the additional habitat patches established by conservation measures may be climatically suitable for too short a time to be used as stepping stones during range shifts. Short-lived species such as butterflies and grasshoppers are probably more affected by high climatic velocities because they lack adequate strategies to persist under adverse climates²¹. An increasing frequency of unfavourable years hence raises their local extinction risk more than those of the mostly long-lived plants in our species set. Grasshoppers, in particular, combine short life cycles with a high degree of ecological specialization. This combination probably makes them highly sensitive to climate effects, but also especially responsive to conservation measures.

We emphasize that the high-level conservation efforts—that is, a conversion of 5% of the study area into high-quality habitat—appears ambitious¹¹. However, even these high efforts would only be able to significantly reduce climate-change-driven regional range loss for a minority of species (Fig. 2). In addition, our business-as-usual strategy—that is, assuming current habitat patterns to remain constant—does not actually presume a worst-case scenario. In fact, land use intensification and expansion of infrastructure have caused severe declines of extensively used habitats in Europe and beyond during the recent decades²². This decline has not yet been halted, neither by the expansion of the protected area network²³, nor by newly introduced regional policies such as the European Union Restoration Goals¹⁶ or the Green Infrastructure strategy¹⁵. Increasing land use demands for biofuel and food production²⁴ additionally suggest that a realistic worst-case scenario might involve further shrinkage of high-quality habitats, and hence even higher vulnerability of species to a warming climate.

Our results are derived from simulations which are necessarily based on simplifying assumptions and coarse parameter estimates, and which certainly neglect important co-determinants of species range dynamics^{18,25}. It is, for example, possible that even our high dispersal distance estimates are too low for some insect species, as they are mainly based on mark-recapture studies in which long-distance flights tend to be under-represented²⁶. Simulations under the two demographic and dispersal parameter sets (Supplementary Tables 2 and 3) suggest that assuming such higher dispersal

distances would have increased the efficiency of management measures for these particular species. However, our main result of considerable range loss under climate warming despite high conservation effort was insensitive to the strong contrast in the two parameter sets that we applied across all model species. It is hence unlikely that assuming still higher dispersal distances for a subset of species would have changed our conclusions qualitatively (Supplementary Fig. 5 and Supplementary Discussion).

Consideration of other modulating factors would have certainly further modified the results quantitatively. In particular, we did not include climate-driven changes to the vegetation in our models. Such changes will probably lag behind climate warming considerably²⁷, but may nevertheless be fast enough to modify local habitat suitability for insect species in the decades to come. Moreover, the spatial grain of our simulations and the way climatic data are down-scaled preclude proper accounting for microclimatic refugia which may mitigate range loss, especially in alpine areas. Additional unaccounted factors such as climatic extremes²⁸ or human-mediated dispersal²⁹ can decrease local species persistence or increase their mobility and thus affect range change. In essence, however, the two sets of parameters used span a broad range of possible species' demography and mobility that should also comprise most effects of these modulating factors on range dynamics.

We conclude that habitat-based measures to mitigate the negative effects of climate warming on species' range sizes are necessary but that their efficiency is limited. Although additional climate change adaptation measures for species are feasible (such as assisted migration programs), these approaches also face severe constraints because they can realistically be implemented for only few charismatic species. Moreover, they may have unforeseen negative consequences for resident biota³⁰. As a corollary, efforts to mitigate climate effects on biodiversity are urgently needed, but are unlikely to be as effective as halting climate change itself.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the [online version of this paper](#).

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Author contributions

S.D. and F.E. designed the study. F.E., S.S. and W.R. compiled the species data. M.K. and D.M. compiled the region and climate data. A.G., J.W., K.H., D.M., M.K. and S.D. performed the analyses. J.W., S.D., K.H. and F.E. wrote the text with further input from all authors.

Additional information

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Competing financial interests

The authors declare no competing financial interests.

Methods

Predictions of range dynamics of the study species were derived from spatially and temporally explicit simulations run in the modelling environment CATS (Cellular Automaton Type Model for simulating plant Spread^{31,18,31}). CATS combines species distribution modelling (SDM) with simulations of the local demography of individual populations and the spatial redistribution of their respective offspring (seeds/eggs). Demographic rates at individual sites at a particular time are assumed to be sigmoid functions of the occurrence probability predicted by SDMs. This sigmoid shape is motivated by the assumption that vital rates are related to physical gradients via a bell-shaped Gaussian function but cannot exceed maxima set by the species' biological traits. The model is spatially and temporally discrete: sites are 100×100 m cells of a contiguous raster representing the study area, and time proceeds in annual steps. Range dynamics result from the impact of changing climatic suitability of sites on local demographic rates, the consequent growth or decline of local populations, eventual extinction from sites that are no longer climatically suitable, or dispersal-mediated establishment at newly suitable sites.

We collected 47,017, 16,348 and 17,138 occurrence records from national recording schemes and biodiversity databases supplemented by literature data for plant, butterfly and grasshopper species, respectively, (Supplementary Table 4). Spatial accuracies ranged from point data up to raster cells of the floristic mapping scheme of Central Europe (=quadrants, 3×5 geographic minutes, approximately 30 km^2 , see ref. 32). We harmonized these data to a resolution of 1×1 geographic minutes ($\sim 2.3 \text{ km}^2$; that is, minute field): more accurate records were assigned to the respective minute field, whereas records of coarser resolution (that is, quadrants) were assigned to a randomly chosen minute field within the respective quadrant. Absences were defined similarly by selecting one randomly chosen minute field in each quadrant without an occurrence record (at whatever resolution). As a consequence, for each species, the sum of presences (see Supplementary Table 5) and absences is equal to the number of quadrants that cover the study area.

We related these occurrence records to six bioclimatic variables³³ by using ensemble forecasts from eight species distribution modelling techniques (GLM, GAM, GBM, ANN, MARS, MAXENT, FDA and Random Forests). Prior to fitting models, bioclimatic variables were downscaled to a 100 m resolution and values at the central 100×100 m site of each minute field were related to species presence and absence records. This downscaling was necessary to adequately represent dispersal processes which are most intense at distances < 1 km for most species. Species-specific climatic suitability raster maps under current climatic conditions and two climate change scenarios—based on decadal climatic series for the Intergovernmental Panel on Climate Change A1B and B2 scenarios—were computed until 2090.

Besides climatic suitability, the performance of study species was also assumed to depend on local habitat types. This dependence was implemented by reducing the maximum population size to 0%, 10% and 100% for unsuitable, marginally suitable and highly suitable habitats, respectively. Habitats were classified to these categories separately for each species based on the literature (see Supplementary Methods). The habitats' spatial distribution across the study area was derived from a fine scaled (spatial resolution 25×25 m, rescaled to 100×100 m) habitat map¹⁹. Conservation strategies were simulated by converting a subset of intensively used habitats (fields, intensive grasslands, conifer plantations) into habitats of high

conservation value. These strategies varied in effort (that is, the proportion of sites converted) and spatial allocation (that is, only in protected areas, in protected areas and connecting corridors and randomly across the landscape).

Local populations were represented by stage-structured cohorts (seeds/eggs, juveniles, adults) with numbers of individuals in particular stages changing according to transition (=demographic) rates (seed persistence, germination, juvenile survival, maturation, fecundity and clonal reproduction in the case of plants; egg-to-adult survival in the case of insects) modulated as functions of SDM-based climatic suitability predictions. In addition, germination, juvenile survival and clonal reproduction were modelled as density dependent (a detailed description can be found in ref. 31).

Plant seed dispersal was modelled by combining three dispersal pathways: for wind dispersal, we parameterized the analytical WALD kernel³⁴ with species-specific seed traits and 10-year wind speed data from a representative weather station. Exo- and endozoochorous dispersal of seeds were based on random-walk simulations of a 'general large mammalian seed dispersal vector' representing a suite of species potentially capable of long-distance dispersal such as red deer, roe deer, chamois or ibex and parameterized by literature data. Seeds are assumed to be uptaken by the walking animal at random and lost again after species-specific times. Ovipositing of insects was modelled by random-walk simulations kept within a species-specific maximum distance.

To test for the effects of changed climate and conservation strategies on range sizes until 2090 we ran CATS for each study species under a full factorial combination of constant current climate and the two climate change scenarios; the nine conservation strategies and a business-as-usual strategy (no conservation strategy implemented); and two sets of demographic and dispersal parameters of each species (to account for uncertainty in parameter estimation). To account for stochastic elements in CATS, we averaged results derived from five replicated runs for further analyses.

We quantified the effect of climate change and conservation strategies on projected range sizes of species as log (range size at 2090/range size at 2010) and log (range size applying a conservation strategy/range size in the business-as-usual strategy) at 2090. These log-ratios ensure that changes in range size (that is, increases or decreases) are symmetric around zero.

For a more detailed description of the modelling environment and set-up see Supplementary Methods.

Data availability. The data that support the findings of this study are available from the corresponding author upon request.

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